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On *Cryptophialus melampygos* Berndt, a Small Boring Barnacle of the Order Acrothoracica Abundant in Some New Zealand Molluscs

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Abstract

AN account is presented of *Cryptophialus melampygos* Berndt, a small boring barnacle of the order Acrothoracica. On wave-exposed shores throughout New Zealand, it extensively erodes the shells of *Perna canaliculus, Haliotis iris* and other molluscs. The female has a pair of small mouth cirri, four pairs of terminal cirri, and a single dorsal filamentary appendage. It has the enormous labrum characteristic of the genus. The internal anatomy is described. Breeding occurs throughout the year. Dwarf males are reduced and pear-shaped, lying in the burrow of the female. The nauplii, which are immobile, show antennules only. Metanauplii, in addition, develop a number of paired appendage rudiments, which vanish at the cyprid stage. The cyprid larva, which leaves the mantle cavity, can crawl but cannot swim. At metamorphosis its antennules and carapace flatten on the surface of a shell. The female that differentiates beneath the cyprid carapace is reversed in dorso-ventral orientation in relation to the cyprid, contrary to the mode of metamorphosis in the primitive thoracican cirripedes (Lepadomorpha).

INTRODUCTION

Crytophialus melampygos is an acrothoracic barnacle that is abundant on certain New Zealand shores. The species is not new, as it was very briefly described by Berndt (1907); but it was subsequently overlooked by workers in this country. A few years ago it was rediscovered by E. J. Batham on New Zealand shores, at about the same time that J. T. Tomlinson noted its record in literature, while carrying out a revision of the order Acrothoracica. The opportunity is now being taken, during Tomlinson's visit to N.Z., to prepare an account jointly.

MATERIAL and METHODS

Abundant fresh and preserved material was available. Fresh specimens remained alive for months *in situ* in mollusc shells maintained in running seawater in the laboratory. Samples were fixed monthly over one year. A few mollusc shells with the barnacles were decalcified with changes of 1% HCl after fixation, after which the barnacles were much more readily removed. A few Bouin-fixed specimens were

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serially sectioned and stained with Mallory. External features were described partly from whole specimens temporarily mounted, partly from specimens briefly boiled in dilute KOH solution. Biological data are based on specimens from Little Papanui, Otago Peninsula.

Systematics

Family CRYPTOPHIALIDAE Gruvel, 1905; Abdominalia Darwin, 1854; Berndt, 1903; Cryptophialidae Berndt, 1907; Barnard, 1925; Tomlinson, 1960; Stubbing, 1961.

Diagnosis: Labrum long, attenuated; mouth cirri atrophied or absent; 3 or 4 pairs of terminal cirri; no anal appendage; alimentary canal with gut teeth and a gizzard; mantle with adhesive discs; lateral bar present; oviducts simple; naupliar stages passed in the mantle cavity; cyprid larva as dispersal phase.

Genus Cryptophialus Darwin, 1854.

Single genus, with the characteristics of the family.

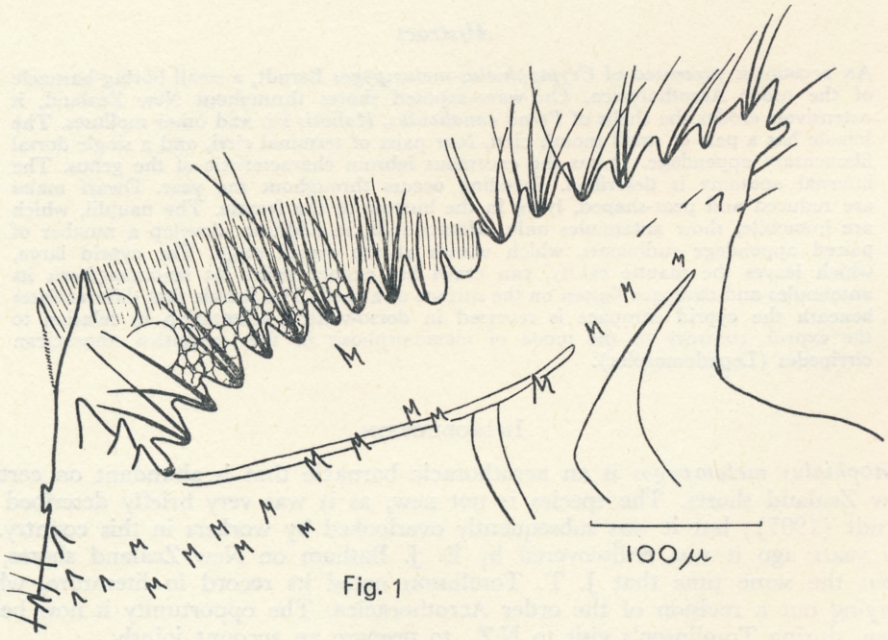


Fig. 1

Fig. 1.—Mantle lips of female of *C. melampygos*, × 225.

Cryptophialus melampygos Berndt, 1907.

Diagnosis: Mouth cirri very reduced; 4 pairs of terminal cirri; one filamentary appendage situated dorsally; mantle aperture with about 20 single teeth and numerous fine setae; lateral bar on each side of the mantle surrounded by small tooth-like spines.

This amends Berndt's original description, which (translated in entirety) is as follows:

"Mantle opening like *Cryptophialus minutus*. Characterised by strong dorso-ventral flattening of the body and by dark pigment accumulations on the cirral hairs and on the last segment of the body. In *Haliotis iris* — New Zealand."

There is little from this description for positively identifying Berndt's barnacle. However, in view of its occurrence in *Haliotis iris* in New Zealand, and its coloration, and as no other acrothoracican has been found to date in N.Z., it seems appropriate to identify the present form as Berndt's *Cryptophialus melampygos*. A more detailed account of the biology and morphology follows.

HABITAT: On rocky shores where there is much water movement, especially those exposed to continuous wave action, this barnacle occurs in extraordinary abundance in a number of mollusc shells. In such a habitat, the shells of the large mussel *Perna* (= *Mytilus*) *canaliculus* Gmelin, by the time they exceed 4cm in length, are usually infested. The barnacle invades the outer surface of the shell, more especially at its anterior end, where abrasion between adjacent shells in a mussel bed removes the horny periostracum and exposes the calcareous layers beneath. *Cryptophialus,* together with several species of boring polychaetes, cause the familiarly-pitted appearance of shells of this mussel (Plate 1, A). Together with polychaetes, these barnacles also frequently corrode the shells of *Haliotis iris* Gmelin. Other mollusc shells in which we have found it less regularly are: on outer Otago Peninsula — *Scutus breviculus* (Blainville), *Lunella smaragda* (Gmelin), *Mytilus edulis aoteanus* Powell (— infrequent), *Aulacomya maoriana* (Iredale) and *Onithochiton neglectus* Rochebrune; at Diamond Harbour, Banks' Peninsula, — *S. breviculus, L. smaragda, Haustrum haustorium* (Gmelin) and *Sypharochiton pelliserpentis* (Q. and G.); near Kaikoura, also in *Lepsithais lacunosus* (Brug.), *Argobuccinum tumidum* (Dunker), and in the barnacle *Elminius plicatus* Gray. In other localities, other molluscs carrying *C. melampygos* include *Sypharochiton torri* (Suter), *Guildingia obtecta* (Pilsbry), *Amaurochiton glaucus* (Gray) and *Neothais scalaris* (Menke), the latter at Piha being a more frequent host than *Perna* for *C. melampygos*. It seems that, on rocky shores with adequate water movement, this barnacle is only to a limited extent selective of mollusc species; a sufficient thickness of exposed calcareous shell being the main requirement. We have not found this barnacle in habitats other than the shells of living molluscs, with the exception of the one record from the barnacle *Elminius plicatus*.

It occurs chiefly at low tide level, but may ascend well into the midlittoral where waves keep this normally wet. Its apparent absence at subtidal levels is indicated by negative results from a comprehensive search of over a hundred large *Perna canaliculus* shells collected from 7 to 8 fathoms by the Coromandel Mussel Company, approximately 2½ miles E.N.E. of Orere Point.

DISTRIBUTION: *C. melampygos* occurs along the length of New Zealand, from North Auckland to Stewart Island, on both east and west coasts. Specific localities from which we have collected or received specimens are: Herekino and Piha, West coast of Auckland province; Matapouri and Leigh, east coast of North Auckland; Mount Maunganui, Bay of Plenty; The Sisters, New Plymouth; Point Halswell, just inside Wellington Harbour heads; immediately south of Westport; at Haumari Bluff and Halfmoon Bay, near and at Kaikoura; at Taylor's Mistake and Diamond Harbour, near Christchurch; at Little Papanui and St. Clair, near Dunedin; and at Halfmoon Bay, Stewart Island. Our thanks are due to Dr W. Ballantyne, Miss M. Dewar, Miss P. Luckens, Miss L. B. Moore and Mr C. Trevarthen for molluscs from additional localities. The above *Cryptophialus* records have all beeen checked by one or other of the present authors.

Limited searching at the Chatham Islands by E. J. Batham failed to show *C. melampygos* on apparently suitable shores, *Durvillea* there lacking the beds of *Perna* that occur round the mainland. The absence of a swimming larval phase in this species may well restrict its distribution.

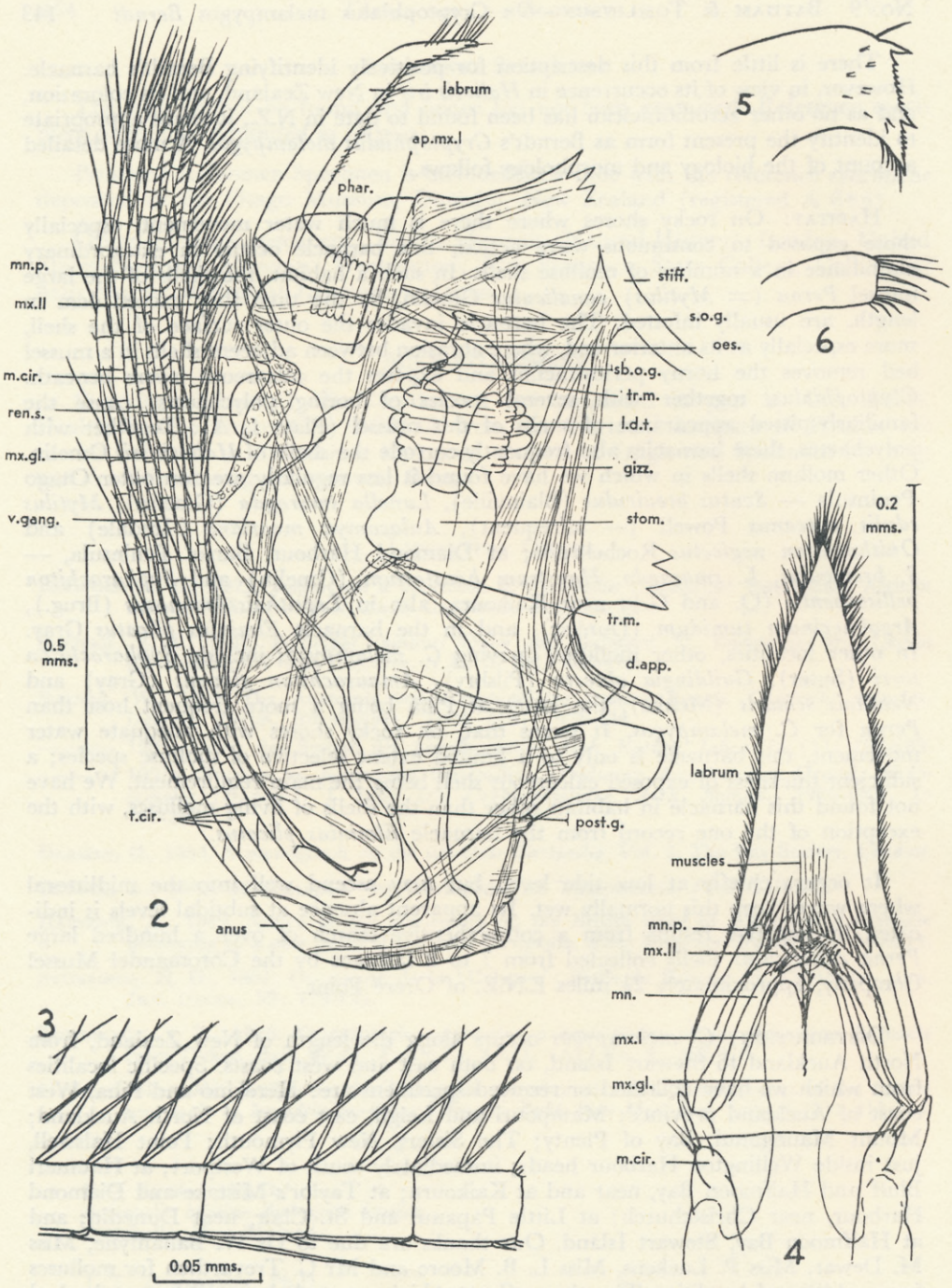


Fig. 2.—Body of female, removed from mantle. Reconstruction, × 63. The terminal cirri bear two pairs of bristles in the inner curvature. They are illustrated unpaired for simplicity. mn.p.—mandibular palp. mx.II—second maxilla. m.cir.—mouth cirrus. ren.s.—renal sac. mx.gl. maxillary gland. v.gang.—ventral ganglion. t.cir.—terminal cirri. phar.—pharynx. ap.mx.I—apodeme for first maxilla. stiff.—stiffener. s.o.g.—supra-oesophagael ganglion. oes.—oesophagus. sb.o.g.—sub-oesophagael ganglion. tr.m.—transverse muscle. l.d.t.—lobes of digestive tract. gizz.—gizzard. stom.—stomach. d.app.—dorsal appendage. post.g.—posterior ganglion. Fig. 3.—Portion of terminal cirrus, showing setation, × 30. Fig. 4.—Mouth-field of female. Lettering as in Fig. 2. Also mx.I—first maxilla. mn.—mandible. × 230. Fig. 5—Mandible, × 230. Fig. 6.—First maxilla, × 230.

ABUNDANCE: *C. melampygos* is frequently abundant, and at times extremely abundant, in the shells of *Perna canaliculus* and *Haliotis iris*. Where infestation is heavy, pits are adjacent (Plate 1, G), and in places the intervening mollusc shell breaks down. A count was made of the number of *C. melampygos* in a shell of *Haliotis iris* from Halfmoon Bay, near Kaikoura, which measured 122 x 89mm. The total was approximately 3,350 female barnacles! Where it thrives, *C. melampygos* is far more abundant than any other acorthoracic barnacle that J. T. Tomlinson has encountered; though Darwin (1854) records that *Cryptophialus minutus* "inhabits, in vast numbers, the shells of the living *Conchorderma peruviana*".

BARNACLE SLITS AND PROTRUSION OF CIRRI

The barnacle slits seen externally in mollusc shells are ovoid in shape (Plate 1, E, F,). The aperture is more parallel-sided than in most Acrothoracica, with the ends rounded rather than tapered. Of 25 recently-vacated barnacle pits in one *Perna* shell, the largest had an orifice of 1.1mm long, 0.6mm wide; whilst the average was 0.75mm long, 0.4mm wide. Twenty apertures from another heavily-infested shell averaged 0.40mm long by 0.23mm wide, whilst the pits beneath averaged 1.9mm x 1.3mm. On breaking open a portion of a mussel shell, it is seen that the pits which the barnacles have excavated are considerably larger than their external orifices would suggest (Fig. 8). For instance, the shell shown in Plate 1, F, was chipped away, revealing 5 pits averaging 1.6 x 1.1mm, as compared with 0.75 x 0.4mm at the surface (cf. F and G, Plate 1).

In each slit containing a live barnacle, the pair of mantle lips can be seen from the outside. These may be tightly closed (Plate 1, E, upper right), slightly open (left), or open with the cirri protruding (centre right). When a mussel shell is left undisturbed in a dish of seawater, many of the barnacles will soon show the cirri protruding and retracting more or less rhythmically. Of 10 specimens each observed continuously for 10 minutes (in seawater between 11° and 16°C), the average number of cirral extrusions and withdrawals per minute, during activity, was 8, whilst the maximum number per minute (at 16°C) was 16. The cirri were protruded sometimes slightly, sometimes extensively without being spread, and at other times were extensively spread in a wide fan, liable to rotate to left or right. Four of the 10 observed specimens continued relatively regular cirral activity throughout the observation period; the other six closed up for periods of minutes before resuming activity.

BREEDING PATTERN

Newly-settled females have a mantle length of 0.2mm. Of 8 females examined from 0.9 to 1.1mm long, only one carried a dwarf male. Most females acquire their first dwarf male (at cyprid stage) when 1.2mm long, and almost invariably carry males from this size upwards. (Seven out of eight females 1.2mm long showed a cyprid on the outside of the mantle sac.) Whilst growing from 1.2 to 1.8mm mantle length, the female steadily increases the number of males from one to as many as six. As she further grows in size, the average number of males remains at about this number, old males being spent and presumably discarded as new cyprids settle on a female.

Although the female acquires her first, immature dwarf male when only 1.2mm long, she does not become ovigerous until 1.6 to 1.8mm in length. On an average, 3 out of 4 females over 1.7mm in length have eggs or larvae in their mantle cavities at all times of year. Monthly sampling shows no indication of a breeding season (Table I). One batch of larvae leave the mantle cavity as actively-walking cyprids before the next batch of eggs is laid.

TABLE I.—Number of females out of 10 sampled, each over 1.7mm long, carrying eggs or larvae. December sample lost. Recorded inshore surface sea temperatures ranged from 8.4° to 15.0°C, at Little Papanui, Otago Peninsula.

Jan.	Feb.	Mar.	Ap.	May	Jn.	Jy.	Aug.	Sep.	Oct.	Nov.
7	8	9	7	8	8	6	8	7	6	7

Since a female acquires her first male well before she reaches egg-producing size, the cyprid developing into the first male presumably comes from another, older female. We have not discovered what determines sex in *C. melampygos*. No obvious differences that might be correlated with sex were noticed in the larvae. Staining of chromosomes by one of us (J. T. Tomlinson) showed them to be so minute that they could not be counted with confidence; so that the presence or absence of a sex chromosome has not been determined.

A mean of 14 eggs per egg-carrying female, 14 nauplii per nauplius-carrying female, and 13 cyprids per cyprid-carrying female was observed. These figures are based on 35 females with eggs, 41 with larvae. Times of developmental stages have not been followed. The maximum number of eggs in one female was 44 (female 2.6mm long), of nauplii, 33 (female 2.5mm), and of cyprids 31 (in a female of 2.7mm). Most of the breeding females were 1.9, 2.0 or 2.1mm long, relatively few exceeding this size. The largest specimen measured was 2.9mm in length. Measurements were based on anaesthetised, formalin-preserved specimens removed from decalcified *Perna* shells from Little Papanui, Otago.

Of 134 females over 1.2mm long, only 3 apparently lacked dwarf males. As males can readily be dislodged in removing a female from even a decalcified pit, it seems that almost all, if not all, larger females carry dwarf males.

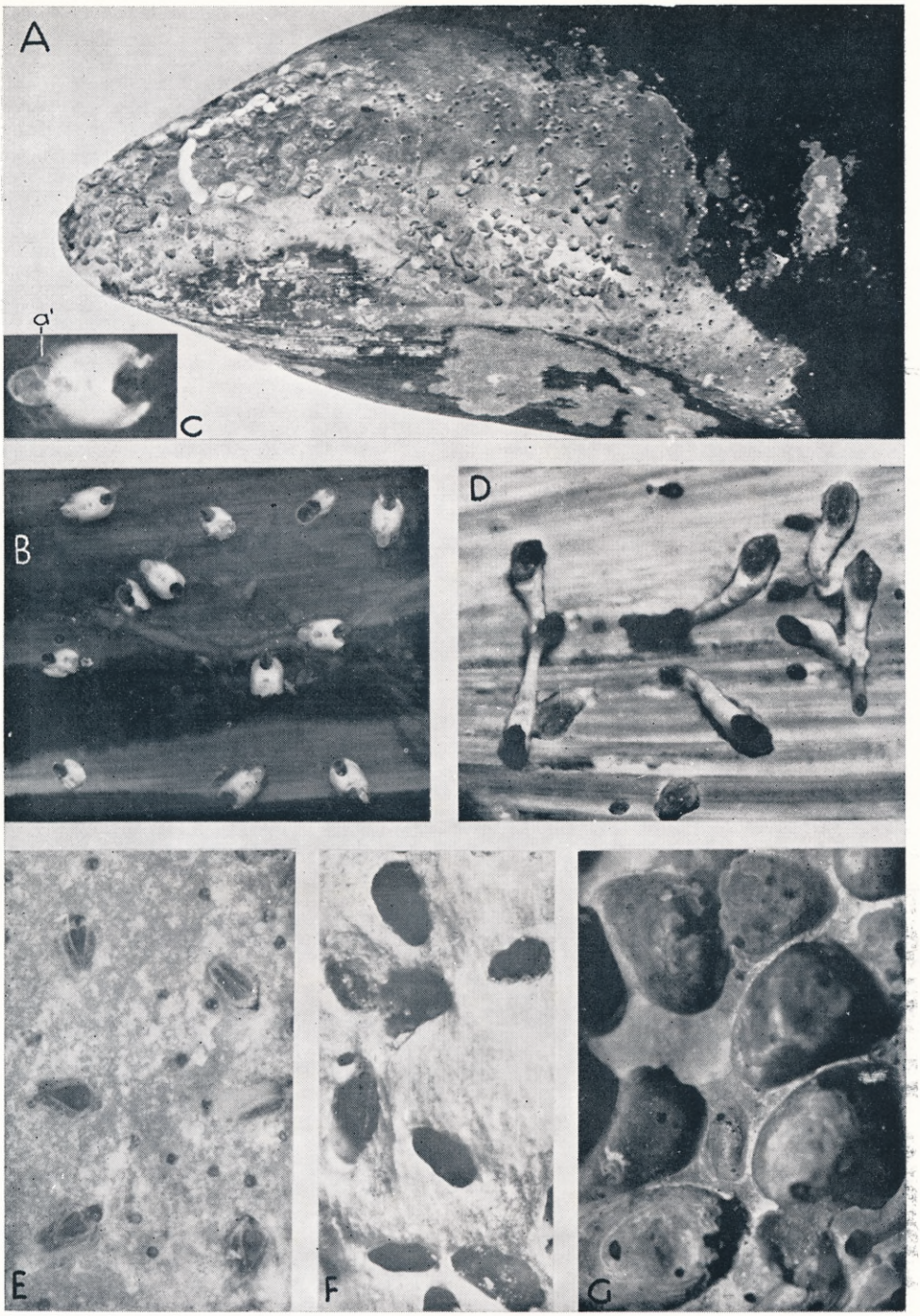
THE FEMALE

The Mantle (Fig. 7) is a very pale reddish-yellow colour, except for a reddish-purple band just below the mantle aperture. This pigment is usually present on the labrum internally as well. A little pigment may be seen on the cirri or on the last segment of the body, as reported by Berndt (1907). The pigment may be intensified by dehydrating and then clearing in xylene.

The lips of the aperture superficially appear smooth, unlike those of other species of the genus. On closer examination, however, a row of about 20 small single teeth or spines, interspersed with more numerous bristles, can be seen to line the edge (Fig. 1). The comb collar typical of the order is present, and may serve to clean the cirri and close the aperture. It is a fine membrane with a comb-like distal edge, and projects inwards from the inner aspect of each lip. At the end of the aperture, whence the cirri protrude, the comb collar doubles back, forming an additional velum below the lips.

The mantle is lightly cemented to the burrow, but several layers of exuviae can accumulate in the cemented area. Several males occur in the upper, apertural portion of the attachment disc. The accumulation of exuviae where the barnacle is cemented to the burrow results in a horny knob in many species, but in this species a knob is not prominent.

Internal bars are present on each side of the mantle, and are symmetrical in details, as heavily chitinized rods extending from the lips to the middle of the mantle, and ending in curved supports each surrounded by an array of teeth. There are about 10 teeth on each flank, those on the inner end being markedly larger. The single inner portion of the stiffening bar near the proximal end of the mantle aperture is similar to that of *C. minutus*. It is hollow, and serves as a muscle attachment for several sets of heavy muscles.



A.—Eroded anterior end of shell of mussel *Perna canaliculus*, showing stages of *Cryptophialus metampygos* infestation, × 1½. Minute white specks at junction of dark and eroded parts of shell (right) are newly-settled females. Small pits (upper centre) are mantle openings of live barnacles. Larger, shallow pits (lower centre and left) are eroded cavities caused by barnacles no longer present. B—*Perna* shell carrying 12 white cypris carapaces overlying early metamorphosing females of *Cryptophialus*, × 16. C.—As last, × 48. a′ – antennules of cypris. D.—Scars on mussel shell sometimes caused when barnacles migrate slightly from point of entry into shell, × 16. Dark ovals represent lips of live barnacles. E.—Six live *C. melampygos* in *Perna* shell, showing barnacle mantle lips open (upper and middle left), closed (upper right), and with cirri extruded (middle right), × 16. (The numerous smaller holes belong to the boring bryozoan *Immergentia irregularis* Silen, 1956). F.—Ovoid pits recently vacated by *C. melampygos*, in *Perna* shell, × 16. G.—Shallow depressions left by *C. melampygos* on *Perna* shell whose surface layers have eroded off. Same scale as last. The larger size of these depressions, as compared with F, reflects the shape of the mantle and narrower lips of the female (cf. fig. 7).

The rest of the mantle is studded with very fine single, double and three-pronged teeth (Fig. 9).

The musculature of the mantle consists of the usual double layer of striated fibre bundles, varying in size and length. Longitudinal bundles extend from the clear area below the lip of the mantle around to the deepest part of the mantle, while about 20 circular muscles radiate out from the area of attachment in the pit. These are predominantly strong and internal near the attachment area, becoming weak and external in the mantle distal from the attachment area. There are 7 to 8 longitudinal bands in the internal set near the attachment area, and 10 to 12 in the external distal set.

The Cirri (Figs. 2, 3). The single pair of mouth cirri is very much reduced and unsegmented. Each mouth cirrus has 3 to 4 terminal bristles. The 4 pairs of terminal cirri are biramous and multi-articulated, on a two-segmented pedicel. Typically the cirri bear two pairs of bristles per segment on the lesser curvature, and a single bristle on most segments on the greater curvature. The former are more uniform in length than is typical for the group, and the latter are more numerous than usual. The single bristles arise from the distal end of the segment. Many are very short, their length being about one-third the width of the cirrus; except for every second to fourth bristle, which is about the same length as those on the lesser curvature (Fig. 3). Segment counts for the terminal cirri have the following range: first terminal cirrus, 12-14; second to fourth terminal cirri, 20-25 segments per ramus.

The Mouth Parts (Figs. 4, 5, 6). The paired mandibles with palps, and the first and second maxillae, are typical for the order; but the long, median labrum is peculiar to the genus. The labrum extends from the upper edge of the mouth to the mantle aperture. Along its edges, and terminally, it carries many fine bristles, but the inner face is free of these. It seems probable that the labrum serves as a limiting membrane for the cirral action, and assists in directing food to the mouth in lieu of the much reduced mouth cirri. It should be noted that acrothoracicans cannot conveniently pass food to the mouth with the terminal cirri, as these are grouped together and do not move effectively in relation to one another, as in the Thoracica. Most acrothoracicans convey food to the mouth by wiping the terminal cirri with the mouth cirri. The Cryptophialidae, however, lack well-developed mouth cirri, but all have a well-developed labrum.

The mandibles (Fig. 5) have 3 major teeth, with fine teeth situated between them. Very fine bristles are present on the edges and face of the mandible. The mandibular palps are long, lying laterally to the mandibles along the edges of the labrum. They are armed with strong bristles on the medial and terminal margins.

The first maxillae are very delicate, without the strong teeth seen in other species. Four bristles and additional very fine hairs are seen on the distal margin.

The second maxillae close the lower mouth field, and are heavily supplied with bristles typical of the order. The maxillary glands are pronounced, and can easily be seen in and below the second maxillae.

The Digestive Tract (Fig. 2). The oesophagus extends dorsally from the mouth parts, through a series of muscular rings presumably serving as a pharynx, and then bends posteriorly to enter the gizzard. It passes around a transverse muscle which is located, with the suboesophageal ganglion, immediately posterior and ventral to the oesophagus. The gizzard is composed of 6 radiating, wedge-shaped portions, with their apices directed inwardly and armed with teeth. The stomach arises immediately posterior to the gizzard, and is divided into large lobes by another tranverse muscle. Highly divided diverticula extend forward to both right and left sides of the stomach just posterior to the gizzard, and ramify into about 8 finger-like lobes directed dorsally and ventrally on both sides of the gizzard. The mass of

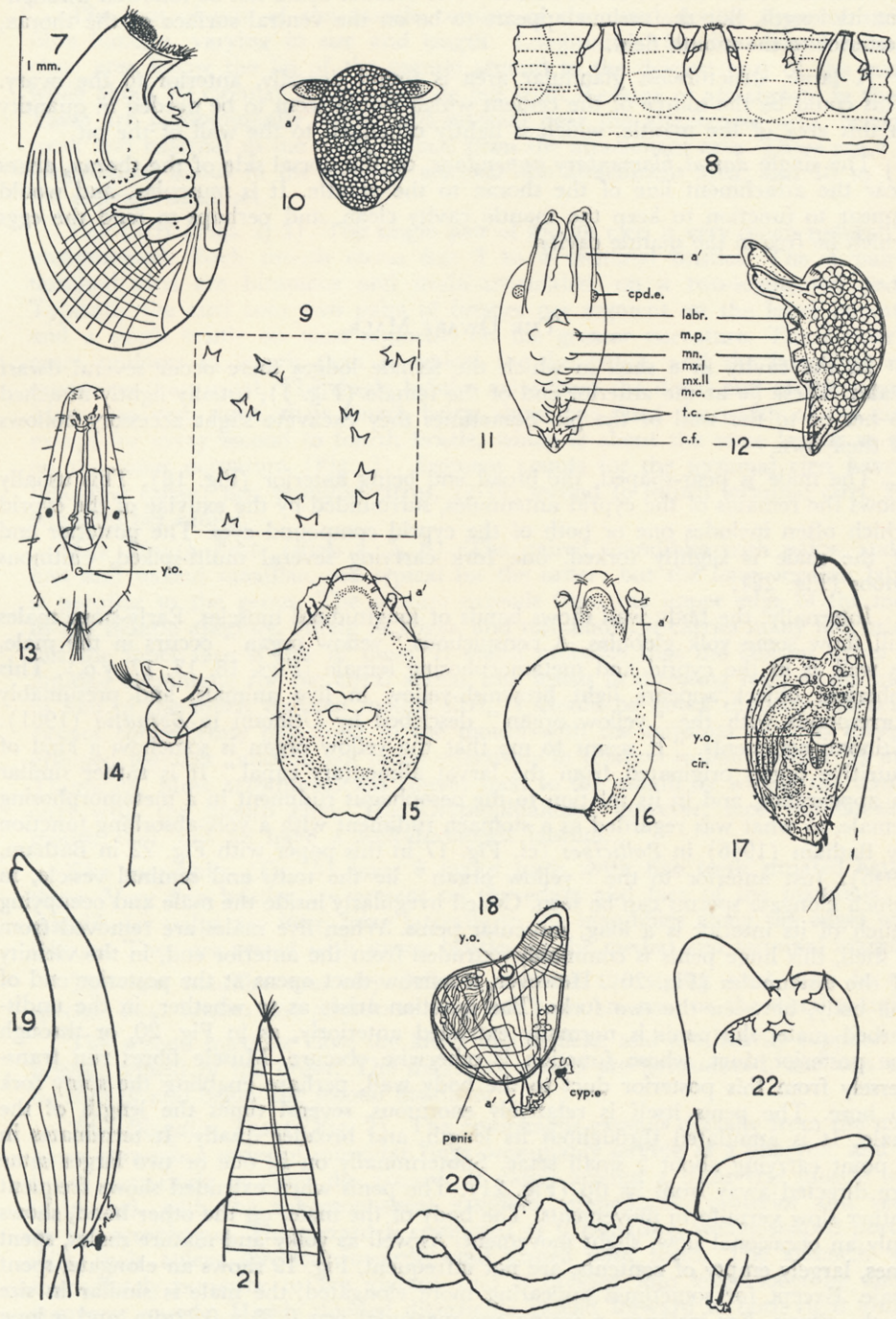
material in the posterior end of the stomach, characteristic of the genus, appears to be composed of large cells resistant to corrosion by 10% KOH. The posterior ganglionic mass lies just ventral to this area of the digestive tract. The intestine extends into the posterior end of the thorax and terminates as a slit-like anus between the two sets of paired thoracic cirri on the dorsal side.

The Nervous System consists of the typical supra-oesophageal ganglion or "brain," sub-oesophageal ganglion, a posterior ganglion, and a ventral ganglion, plus more-or-less clearly defined tracts connecting these major ganglia with local swellings which may represent minor ganglia. The supra- and sub-oesophageal ganglia lie respectively immediately above and below the oesophagus, where the latter makes a sharp bend into the gizzard. The posterior ganglion rests against the ventral side of the posterior end of the stomach. Between the posterior and sub-oesophageal ganglia, a large mass of glandular cells, with associated nerve fibres, lies in the extreme ventral side of the female. No eyes and no other special sense organs were seen.

The Excretory System is represented by two typical structures: the maxillary gland and the renal sacs, both in the area of the mouth parts. The maxillary gland is a large, paired glandular mass extending from the second maxillae along the mid-line posteriorly, bending laterally and forward into ridges bearing the mouth cirri. The renal sacs are clear, paired vesicles immediately behind the large maxillary glands, around which these glands curve. No ducts were observed.

The Muscular System is complex. Fig. 2 shows only the major muscle strands. The state of knowledge of comparative musculature does not allow a conclusive assignment of names to these muscles. A major set of muscles, associated with the stiffening bar (cf. Darwin's *C. minutus*) extends from the dorsal end of the lips of the mantle aperture internally along the dorsal side of the mantle, and continues in a heavy muscle with associated tendon-like fibres to the dorso-posterior mantle wall. Arising from this stiffener are several bands of muscles, particularly prominent ones going to the pharynx and oesophagus, and to the dorsal wall of the thorax, especially where it attaches to the mantle and the dorsal appendage. Two transverse muscles have been noted above, associated with the digestive tract. One crosses just posterior and ventral to the oesophagus where the latter bends into the gizzard, and one is in the area of the ventral side of the stomach. These transverse muscles lie not dorsal to the gut, but ventral to it, as in the thoracican *Ibla,* a genus showing several other resemblances to the Acrothoracica. In all other Thoracica, the adductor passes dorsal to the gut. Two large and one somewhat smaller bands of muscle extend into the thorax and cirri, and are used to manipulate these food-gathering appendages.

Fig. 7.—Female, × 18, showing transverse and longitudinal muscles of mantle, attachment region (at right), and 4 dwarf males, the lowest in the act of metamorphosing. Fig. 8.—Section of *Perna* shell, × 6, showing several *Cryptophialus in situ,* and the burrows (dotted) of others. Fig. 9.—Portion of mantle, showing boring spines, × 230. Fig. 10.—Nauplius packed with yolk globules, × 68. a′—antennules. Fig. 11.—Metanauplius, ventral view, yolk globules omitted, × 68. Fig. 12.—Metanauplius, lateral view, × 68. a′—antennules. labr.—labrum. cpd.e.—compound eye. m.p.—presumed mandibular palp. mn.—presumed mandible. mx. I.—maxilla I. mx. II.—maxilla II. m.c.—mouth cirrus. t.c.—4 pairs terminal cirri. c.f.—presumed caudal furcae. Fig. 13.—Cypris, ventral view, × 68. A few yolk globules omitted. y.o.—yellow organ. Fig. 14.—Cypris antennule, × 240. Fig. 15.—Attached cypris carapace over young female, × 63. (cf. with Plate 1, B and C). Fig. 16.—Metamorphosing female rudiment under attached cypris carapace, viewed ventrolaterally, × 68. Antennules and setae still on cypris carapace. Rudiment already has boring spines. Fig. 17.—Longitudinal sagittal section of young female rudiment, × 112. cir.—cirri. y.o.—yellow organ with oesophagus forming below it. Fig. 18.—Dwarf male, × 68. y.o.—yellow organ. cyp.e.—compound eye of cypris. a′—antennules. Fig. 19.—Elongated, spent male, × 68. Fig 20.—Dwarf male with penis extruded, × 68. (annulations along penis omitted). Fig. 21.—Tip of penis, × 240. Fig. 22.—Forked posterior end of dwarf male, one fork with spines, × 240.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The Ovary is situated in the dorsal mantle area immediately above the line of attachment of the thorax to the mantle. The oviduct could not be followed throughout its length, but the atrium appears to be on the ventral surface of the thorax, posterior to the mouth field.

A large, structureless glandular area is found dorsally, anterior to the ovary. This could be the source of the cement which would seem to be needed in quantity in this area of the mantle, which is lightly cemented to the wall of the pit.

The single *dorsal filamentary appendage,* on the dorsal side of the thorax, arises near the attachment line of the thorax to the mantle. It is muscular, and would appear to function to keep the mantle cavity clean, and perhaps to tend the eggs which lie free in the mantle cavity.

The Dwarf Male

In the cavity in a shell in which the female lodges there occur several dwarf males. These lie at the anterior end of the female (Fig. 7), usually lightly attached to her or to the wall of the pit. Sometimes they excavate slight accessory hollows of their own.

The male is pear-shaped, the broad end being anterior (Fig. 18). This usually shows the remains of the cyprid antennules, surrounded by the exuviae of the cyprid which often includes one or both of the cyprid compound eyes. The posterior end of the male is slightly forked, one fork carrying several multi-spiked, chitinous knobs (Fig. 22).

Internally, the body wall shows bands of longitudinal muscles. Early-stage males still show some yolk globules. A conspicuous "yellow organ" occurs in the male, as well as in the cyprid and metamorphosing female (Figs. 18, 13, 17, y.o.). This spherical object appears light brownish-yellow in live animals, and presumably corresponds with the "yellow organ" described by Utinomi in *Berndtia* (1961). Utinomi comments, "It seems to me that the yellow organ is somehow a kind of nutritive organ originated from the larval alimentary canal." It is rather similar in appearance, and in its relation to the oesophagus rudiment in a metamorphosing female, to what was regarded as a stomach rudiment with a yolk-absorbing function by Batham (1946) in *Pollicipes* (cf. Fig. 17 in this paper with Fig. 22 in Batham, 1946). Just anterior to the "yellow organ" lie the testis and seminal vesicle, in which elongate sperms can be seen. Coiled irregularly inside the male and occupying much of its interior is a long, muscular penis. When live males are removed from a shell, this huge penis is commonly extruded from the anterior end, in the vicinity of the antennules (Fig. 20). However, a narrow duct opens at the posterior end of the body, between the two forks. The question arises as to whether, in the undisturbed male, the penis is normally extruded anteriorly, as in Fig. 20, or through the posterior duct, whose function is otherwise obscure. Muscle fibres run transversely from this posterior duct to the body wall, perhaps enabling the spiny fork to bore. The penis itself is relatively enormous, several times the length of the male. It is annulated throughout its length, and broader disally. It terminates in a point carrying about 5 small setae. Subterminally on it, one or two larger setae are directed away from its tip (Fig. 21). The penis when extruded shows frequent rather slow vermiform movements. The body of the male, on the other hand, shows only an occasional slow, slight movement. As well as yolky and mature males, spent ones, largely empty of contents, are not infrequent. Fig. 19 shows an elongate, spent male. Except for sometimes appearing more elongated, the male is similar in size to the cypris. For instance, a young one measured was 0.38 x 0.22mm, and a long one was 0.62 x 0.22mm. This is to be expected in the absence of a food canal, as the male's organs are derived from the embryonic yolk.

DEVELOPMENTAL STAGES

The *eggs* are oval, and average 0.26 x 0.21mm, with but slight variation. They lie free from one another in the mantle cavity. Yolk globules largely mask details of embryonic development externally. However, the late embryo shows lobed paired antennules, at this stage held pointing backwards by the enveloping egg-case.

The reduced *nauplius larvae* (Fig. 10) are retained in the mantle cavity of the female. Yolk globules are conspicuous. The earlier stages are broad, with the antennules directed laterally. No trace was seen of antennae, mandibles or a median nauplius eye. The almost ovoid body has a slight protrusion posteriorly. In later naupliar stages the body narrows slightly, and the antennules become directed more anteriorly. The number of moults involved has not been traced. Ten live naplii averaged 0.32mm in length (excluding the antennules), and 0.20mm across. Later nauplii are slightly longer and narrower than earlier ones.

The *metanauplius* (Figs. 11, 12), like the nauplius, is packed with yolk globules and immobile. The antennules by now have bulbous tips. Ventrally, behind the large antennules, a labrum and 10 paired rudiments are discernible in late metanauplii. The sixth to ninth pairs, of which the ninth and sometimes the eighth are biramous, are backwardly directed and obviously seem to be the forerunners of the terminal cirri. The tenth pair, uniramous and placed close together, are provisionally identified as caudal furcae and vestigial abdomen. The small fifth pair are presumably mouth cirri. The slightly larger rudiments, passing forwards from these, would thus be second maxillae, first maxillae, mandibles, and either second antennae or mandibular palps, more likely the former.

The tentative identifications of these immobile metanauplian appendages are due to the curious fact that, on metamorphosis to the cyprid stage, all ten paired rudiments disappear!

At or just before the change to cyprid, the paired compound eyes begin to become pigmented.

Metamorphosis from metanauplius to cyprid: The anterior end of the carapace, folded under in the metanauplius, elongates considerably. The antennules become mobile, showing the characteristic cyprid sucker disc. The metanauplius cirral rudiments are withdrawn, but from their site long bristles protrude posteriorly. The larva becomes more transparent.

The *cyprid larvae* (Fig. 13) differs from a typical cirripede cyprid in being flattened dorso-ventrally. The carapace is narrower anteriorly than posteriorly. It carries a number of setae, some stout, some more slender, arranged fairly regularly in pairs, with but slight variation among individuals. Ventrally the carapace is wide open for the anterior two-thirds of its length, in which the antennules lie. Posteriorly there is a deep opening, through which emerge 4 long and 2 shorter mobile setae. Between the antennules and the posterior setae, the body lies close to the surface ventrally, but the two carapace margins can just be detected, as figured. The edges of the carapace are mobile and flexible. Dorsally the carapace also carries a few setae, though these are less conspicuous than the larger ventral ones. The carapace shows a pattern of pentagons and hexagons, presumably reflecting underlying epithelial cells. The two compound eyes are pigmented black. A "yellow organ" lies medianly a little posterior to them. A few yolk globules (not shown in Fig. 13) were still present internally, and no food canal was discerned at this stage. For the rest, the internal structure largely centres round the stout musculature to the apodemes of the antennules, which are now active. Their terminal discs (Fig. 14) adhere strongly to a glass pipette or metal instrument. The cyprid larva walks rather deliberately on its antennules, holding the body parallel to the

substratum. When walking, the 4 long posterior setae, and also the 3 large ventral pairs (placed one pair just in front of the eyes, two pairs behind them), are pointed downwards, and prop the body behind. The posterior setae are mobile, both antero-posteriorly and laterally. However, they do *not* show the kicking, swimming movements that thoracic cirripede cyprid legs show, and no trace of cirri was discerned in the cyprid stage, either in live animals or in sections. When these *Cryptophialus* cyprids were raised from the bottom in a dish of seawater, they drifted passively down again, and could not be induced to swim.

These cyprid larvae have been found chiefly in the mantle cavities of females, but are also at times seen crawling on the surfaces of *Perna* shells, or on the outsides of *Cryptophialus* females in their pits. They thus represent the dispersal phase for the species, but it is a free-crawling and not a free-swimming larval phase.

The average size of the cyprid is 0.53 x 0.23mm, the largest of 12 specimens measured being 0.56 x 0.26mm, the smallest 0.50 x 0.20mm.

Comparisons: The nauplius is close to that of *Cryptophialus minutus* (Darwin, 1854), although its posterior process is less pronounced. Both these non-free-swimming nauplii contrast sharply with the characteristically cirripedian nauplius of the acrothoracican *Trypetesa* (= *Alcippe*) *lampas,* that has the usual cirripedian biramous antennae and mandibles, fronto-lateral horns and median eye (Hancock, 1849). The *C. melampygos* cyprid is more typically cirripedian. It differs from that of thoracic cirripedes, but resembles the *Cryptophialus minutus* cyprid, in the dorso-ventrally flattened carapace with setae on it, and in the absence of cirri. It differs from *C. minutus* chiefly in the anterior prolongation of the carapace. Both these two species (unlike other Acrothoracica) are liable to be extremely abundant in the shells of the animals in which they occur. This abundance in a suitable host is presumably due to the fact that, in both species, the dispersal phase can only crawl and not swim, and thus usually settles close to its parent.

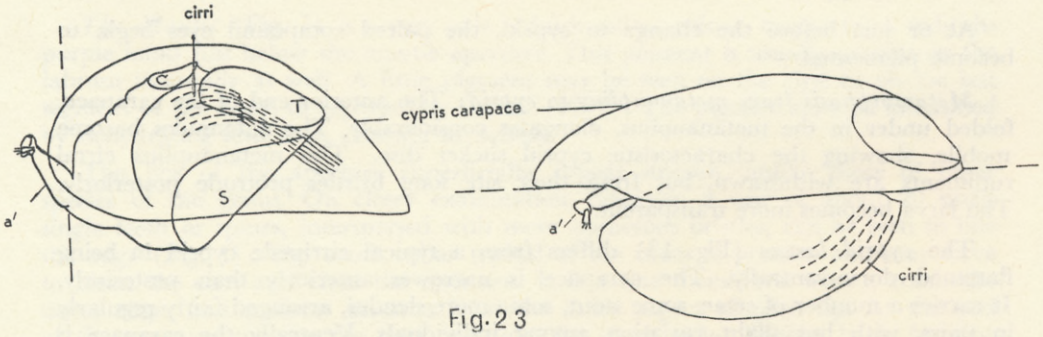

Fig. 23

Fig. 23.—Lateral views of newly metamorphosed adults in relation to cypris carapaces. Left, in thoracic cirripede (*Pollicipes spinosus*), × 60; right, in *Cryptophialus melampygos,* × 100. Note how, when cyprises are similarly orientated, adult cirri in *Cryptophialus* are mirror-image of those in a thoracic cirripede. a'—antennules. Broken line indicating substratum shows that, whereas thoracic cirripede cypris is at right-angles to this, *C. melampygos* cypris lies flat, parallel, on it. Later, in *Cryptophialus,* the anterior end of the female sinks deeper into the shell, so that the resting position of the cirri is at right-angles to the shell surface and not at angle shown.

SETTLING OF CYPRID TO BECOME A FEMALE

(Figs. 15, 16 and 17 and Plate 1, B and C)

The cyprid larva attaches itself to a shell surface by its antennules, and flattens its carapace on the shell, dorsal surface uppermost. Beneath the protection of the cyprid carapace, metamorphosis occurs. The cyprid musculature de-differentiates,

and the animal becomes an ovoid cell mass under the carapace. The ovoid mass or female rudiment promptly secretes chitinous spines (Figs. 16, 17), and transverse and longitudinal wall muscles are formed in what will become the mantle. A specimen dissected out at this stage is an actively squirming, glistening ovoid mass, equipped to begin boring (Fig. 16). Internally, 4 pairs of cirri can be seen differentiating, and a mantle cavity forming (Fig. 17). The extraordinary feature about this metamorphosis, as compared with that of a thoracic cirripede such as *Pollicipes* (Batham, 1946), is that these cirri are directed postero-dorsally to the cyprid, and not postero-ventrally. Thus the relation of the adult to the cyprid is here a mirror-image of the relationship in a Lepadomorph thoracic barnacle (Fig. 23). One way for this to be achieved would be by torsion of the female rudiment under the cyprid carapace. However, this seems improbable, as an early-stage rudiment, still spread along the carapace inside, already shows the postero-dorsally directed cirri (fig.17). Perhaps it is the complete disappearance of all paired limbs in the cyprid (except the antennules which become functionless in the adult) that permit this surprising reversal of orientation at metamorphosis.

Large spines at the posterior end of the female rudiment erode the overlying region of the carapace, making an aperture through which the cirri can protrude as soon as the mantle lips form (Fig. 17; Plate 1, C). The squirming and boring of the female rudiment cause flaking off of granules of calcium carbonate from the host shell. These become packed under the cyprid carapace, giving it the appearance of a glistening white cap (Plate 1, B). Anteriorly the cyprid carapace remains transparent, and at its sides the two now-empty antennules can be discerned (Plate 1, C; Figs. 15, 16, a′).

It has been considered that acrothoracican cirripedes lose their antennules at metamorphosis, differing in this respect from the Thoracica. Hence we call attention to their retention for some time after metamorphosis of the female, on the surface of the host shell, in *Cryptophialus melampygos.*

RELATIONSHIPS

The family Cryptophialidae and the genus *Cryptophialus* are clearly distinguishable from other families and genera of the order Acrothoracica. The other families are distinguished from one another by two clear features: the number of terminal cirri, and the presence or absence of caudal appendages. Cryptophialidae has no caudal appendage, but it is the only family in the order whose members have a variable number of terminal cirri — either three or four pairs. Furthermore, the variability shown in the presence or absence of mouth cirri is unique. This variability may give grounds eventually for splitting the family, or it may reduce the importance of the characteristic in other families. The most obvious positive character shown by all species of *Cryptophialus,* and not occurring in other Acrothoracica, is the enormous elongation of the labrum.

Cryptophialus melampygos shares only with *C. turbonis* Barnard the four pairs of terminal cirri. The other described species all have three pairs. *C. melampygos* shares with *C. minutus* Darwin and *C. variabilis* Stubbings the presence of mouth cirri; in *C. coronatus* Tomlinson they are lacking, while the feature is uncertain in *C. longicollatus* Berndt, 1907a, and *C. turbonis. C. melampygos* shares only with *C. variabilis* the single dorsal body appendage, the other species having two.

The genus *Cryptophialus* is chiefly of southern hemisphere distribution. *C. minutus* occurs in southern Chile, *C. turbonis* is in South Africa, *C. longicollatus* is in Mauritius and *C. melampygos* occurs throughout New Zealand. Two species just cross the equator in West Africa, namely *C. coronatus* recorded from Dakar and *C. variabilis* from Nigeria. The genus is found chiefly in mollusc shells.

To date, *Cryptophialus melampygos* is the only acrothoracic barnacle recorded from New Zealand.

REFERENCE SPECIMENS

The type cannot be found and hence has not been examined. Reference specimens have been deposited as follows:

Principal Reference Specimen is included in a tube with the reference specimens deposited in the Otago Museum, Dunedin, New Zealand (registered A 64.4).

Other reference specimens: British Museum (Natural History), London; United States National Museum, Washington; San Francisco State College, California; Seto Marine Biological Laboratory, Japan.

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